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LOCALIZATION AND RESPONSES OF NEURONES IN THE PARIETO-INSULAR VESTIBULAR CORTEX OF AWAKE MONKEYS (*MACACA FASCICULARIS*)

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SUMMARY

1. In four Java monkeys (*Macaca fascicularis*) 152 vestibular neurones were recorded in the parietal cortex located in the upper bank of the lateral sulcus near the posterior end of the insula. We called this region parieto-insular vestibular cortex (PIVC). PIVC extends about 6–8 mm in the anterior–posterior direction from the posterior part of the insula into the retroinsular region (stereotaxic co-ordinates: anterior 4–12 mm, lateral 16–19 mm and vertical 3–6 mm).

2. About two-thirds of the neurones recorded from this region responded to vestibular stimuli; the non-vestibular neurones responded predominantly to somatosensory stimulation of the neck and shoulder region. The PIVC area is a polysensory field, since almost all vestibular neurones were also activated by somatosensory and visual stimuli. Large-field optokinetic stimulation was the most effective visual stimulus.

3. With vestibular stimuli, responses to angular acceleration were dominant; steady tilt in darkness rarely led to any change in neuronal spontaneous activity. Of sixty-four neurones tested by rotation in more than one plane, fifty-four responded to excitation of semicircular canal receptors aroused by rotation in more than one of the three experimental planes (roll, yaw, pitch). Compared with vestibular brain stem units PIVC neurones discharged with a higher variability.

4. In the responses to horizontal rotation of the animal 38% type I, 53% type II and 9% type III units were recorded (classification according to Duensing & Schaefer, 1958). The gain measured with horizontal sinewave rotation was lower by a factor of about 4 in PIVC neurones as compared with the responses of vestibular neurones in the brain stem or thalamus (VPL). The phase response characteristics and the gain increase with increasing sinewave stimulus frequency, however, were in the same range as observed in neurones of the afferent vestibular system.

5. When the vestibular responses to sinusoidal rotation were tested in all three experimental planes (yaw, roll, pitch), the response strength as expressed by the amplitude of the peristimulus time histograms (PSTHs) differed for the three

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rotational planes. For different units the relative sensitivity to rotation in each of the three planes also differed. We concluded from this observation that different PIVC units had different optimum sensitivity planes for rotation with respect to the head co-ordinates, whereby all possible planes are represented.

INTRODUCTION

Compared with our knowledge on cortical processing of visual or auditory signals (e.g. Hubel & Wiesel, 1977; Merzenich, Andersen & Middlebrooks, 1979; van Essen, 1979; Hubel & Livingstone, 1987), there are very few studies available describing the vestibular cortical representation. In man the localization of a cortical vestibular area is controversial. Foerster (1936) reported that when stimulating the cortical surface electrically during brain operations in conscious patients, a sensation of turning around could be elicited when an area located deep in the intraparietal sulcus and bordering on the somatosensory association areas 2, 5 and 7 was stimulated. Penfield (1957) rarely found vestibular sensations induced by electrical stimulation of the parietal cortex, but the vast majority of vestibular sensations reported by his patients were provoked by stimulation of a region located deep in the lateral sulcus around the superior temporal gyrus, bordering on the auditory areas. More recent studies summarizing reports on vestibular aurae in epileptic patients (Smith, 1960) or measurements of the regional cerebral blood flow during vestibular stimulation (Friberg, Skyhoj, Paulson & Lassen, 1981; Friberg, Olsen, Roland, Paulson & Lassen, 1985) also indicated the existence of a vestibular cortical area in the lateral sulcus region located between the auditory and the somatosensory cortex.

Interestingly, neurophysiological studies in monkeys have also revealed cortical vestibular projection areas in different regions. In addition to the vestibular projection to area 3a (Ödkvist, Schwarz, Fredrickson & Hassler, 1974; Akbarian, Berndl, Grüsser, Guldin, Pause & Schreiter, 1988), Fredrickson, Figge, Scheid & Kornhuber (1966) discovered, by means of evoked potential recordings, a vestibular field in the Rhesus monkey located around the tip of the intraparietal sulcus. Single-unit recordings (Schwarz & Fredrickson, 1971; Fredrickson, Kornhuber & Schwarz, 1974; Büttner & Buettner, 1978) confirmed this location. It was named area 2v, being located at the border of the area 2 of Brodman (1905) in the immediate vicinity of areas 5 and 7. This region most probably corresponds to the vestibular field around the intraparietal sulcus in man, as described by Foerster (1936).

In the present report the localization of a 'new' cortical vestibular field and the neuronal responses to vestibular stimulation will be described. This area of monkey cortex is probably homologous to the vestibular area described by Penfield & Rasmussen (1957) in man. In a following paper the interaction of vestibular responses with those evoked by somatosensory and visual stimuli will be discussed (Grüsser, Pause & Schreiter, 1990). Short reports on the work in the present paper have been given at two scientific meetings (Grüsser, Pause & Schreiter, 1982, 1983).

METHODS

Recordings from the cortical vestibular area in the retroinsular and insular region, called hereafter parieto-insular vestibular cortex (PIVC), were performed in four untrained adult Java

monkeys (*Macaca fascicularis*, 2·5–5·0 kg body weight). Microelectrode recordings were conducted in the left hemisphere of each animal.

Preparations

The surgery necessary for implantation of the base of the chronic stereotaxic device, the electrodes for DC electro-oculographic recordings (EOG) and an aluminium crown was performed under deep pentobarbitone anaesthesia: 7 mg kg^{-1} ketamine hydrochloride I.M. and 45 mg kg^{-1} sodium pentobarbitone I.V. were administered initially followed by a 16 mg kg^{-1} h^{-1} sodium pentobarbitone infusion through a catheter in the femoral vein.

Five Ag–AgCl ball EOG electrodes 2 mm in diameter were fixed with dental cement in holes drilled into the bone of the orbit around the right eye (four electrodes) and on the outer canthus of the left orbit (one electrode). A trephine hole of 30 mm diameter was drilled into the left parietal bone and the support for a Kopf hydraulic microdrive was implanted above this hole parallel to the horizontal stereotaxic plane, as defined by the external auditory meatus and the lower rim of the orbits. In addition, a plug for the EOG electrodes and an aluminium crown similar to that described by Friendlich (1973) were fixed by means of screws and dental cement to the skull. As a rule, 4–6 weeks later the screws had to be tightened (short general anaesthesia). Systemic analgesics (pentazocine, 0·25 mg I.M. per day), and systemic and local antibiotics were administered on the first and second day post-operatively. After the operation the animals were kept on a heating pad for a couple of hours and then returned to their cages.

Recordings

After a post-operative recovery period of 3–4 days, the experiments were performed for 2–4 months, 4 days a week. Each experiment lasted 4–6 h. The head of the animal was fixed by means of the crown to a device connected with a specially designed monkey chair. The chair was placed on an experimental turntable in a chamber separate from the recording equipment, providing sufficient attenuation of laboratory noise (about −30 dB) and also totally shielded optically. The animal sat in a comfortable position with legs and arms either fixed to adaptable, upholstered armrests or unrestrained, restricted only by the sides of the chair. The microdrive was protected by a 30 cm diameter Plexiglass disc fixed to the head holder (Fig. 1) to prevent the animals from reaching it with their free hands.

Horizontal and vertical DC electro-oculograms (0–100 Hz bandwidth) were monitored continuously. For horizontal EOG calibration, the nystagmus slow-phase angular velocity obtained on rotation of the animal in the light inside of the striped cylinder at 40 deg s^{-1} was used. More recent studies with eye position recordings by means of the electromagnetic search coil technique have revealed that these calibration estimates were about 3–5% above the 'real' values.

The action potentials of single neurones were recorded by means of glass-coated tungsten microelectrodes with a tip diameter of about 1–2 μm and a non-insulated part of up to 10 μm length with an impedance of 1–8 MΩ at 1000 Hz. Conventional high-impedance preamplifiers and oscilloscope amplifiers were used for signal amplification. The stereotaxic co-ordinates of the respective microelectrode tips were set (the cylinder centre was anterior +5 mm, lateral +10 mm) according to the atlas of Winters, Kado & Adey (1969).

All bioelectrical data and stimulus signals were stored by means of a 7-channel FM-analog tape-recorder. Simultaneously a 6-channel ink writer (modified Siemens Cardirex) was used for continuous recordings of unit activity, horizontal and vertical EOG, automatically measured instantaneous impulse rate (Eckmiller & Petsch, 1975) and two other selected stimulus signals. The behaviour of the monkey was monitored with a video camera and was stored on videotape in addition to a second videosignal from a camera in front of a 2-channel oscilloscope. These two channels usually displayed the action potentials recorded by the microelectrode and the horizontal EOG, which were later analysed when animal behaviour was compared with single-unit activity.

Vestibular stimulation

The aluminium crown served to fix the head tightly to a special head holder aligned to the vertical axis of the system. A special device either prevented any head movements or allowed voluntary or passive head rotation in the horizontal plane. The head position was measured by means of a potentiometer connected to the vertical axis of the head holder.

The 'horizontal' stereotaxic plane (external auditory meatus–inferior rims of the orbitae) was inclined forward by about 10 deg relative to the ground horizontal plane. Thus the horizontal semicircular canals were not exactly aligned to the plane of horizontal rotation. This compromise was made to prevent the monkey's field of gaze from being shifted too far downwards. The

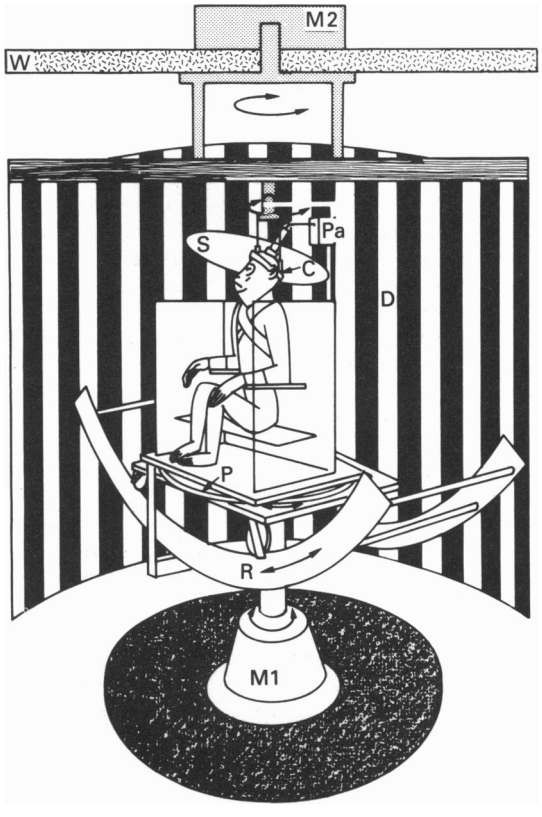

Fig. 1. The experimental set-up. The monkey sat in the rotating chair, surrounded by a striped cylinder. Part of the stripe drum (D) was removed. Cylinder and chair rotation could be coupled to each other or were turned independently by microprocessor-controlled servomotors (M1, M2). Except for the preamplifiers (Pa), all electrical recording and control equipment was placed outside the acoustically shielded experimental room. For reasons of clarity, the forward inclination of the head is not shown. W = wall of the experimental room, R = semicircular rails for rotation in pitch and roll direction, P = rotatable platform, C = crown to fixate the monkey head, S = Plexiglass shield.

turntable was rotated by a servomotor controlled by a programmable microprocessor. The position of the turntable was recorded by an optical goniometer from which the signals were fed back to the amplifier system driving the servomotor. In later experiments the stimulus program was prerecorded on analog tape and fed directly into the amplifier system controlling the servomotor.

We used sinusoidal rotation around the vertical axis ('yaw' rotation) at frequencies between 0·1 and 1 Hz. Amplitudes and maximum velocities similar to those used by Buettner, Büttner & Henn (1978) were chosen. The most frequently used fixed stimulus parameters were: 0·1 Hz (112 deg), 0·2 Hz (56 deg), 0·5 Hz (14 deg), 1·0 Hz (3·5 deg). The respective maximal velocities were 70, 70, 44, 22 deg s^{-1} and the corresponding maximal accelerations 44, 88, 140, 140 deg s^{-2}. For vertical sinewave stimulation ('pitch' or 'roll') the frequency was 0·7 Hz, the maximal amplitude 15 deg, the maximal velocity 66 deg s^{-1} and the maximal acceleration 290 deg s^{-2}. Vestibular stimulation

was also accomplished by suddenly stopping after horizontal rotation of a constant angular velocity of at least 30 s (maximum deceleration -200 deg s^{-2}). In some of the experiments 'trapezoidal' horizontal velocity profiles with constant acceleration or deceleration stimuli between selected velocities were used. Sinusoidal rotation around a fronto/occipital axis ('roll') and a bitemporal axis ('pitch') with an amplitude up to ± 25 deg could be easily achieved since the monkey chair was mounted on a small rotation platform which could be moved on steel rails in the shape of a circle sector of ± 30 deg (Fig. 1). The centre of roll and pitch rotation was the monkey's head centre at eye level. Once sinusoidal movement around one of the two axes mentioned had commenced, pushing the chair slightly was sufficient to maintain a sinusoidal positional change at 0·7 Hz, corresponding to the resonant frequency of the system, since friction was minimal between the rolls on the base of the monkey chair and the steel rails.

Visual and optokinetic stimulation

The simplest visual stimuli were small objects appealing to the monkey (e.g. raisin, peanut, etc.) fixed on a thin plastic stick and moved within as well as outside of the grasping range of the animal. For more systematic visual stimulation a transparent vertical 90×90 cm projection screen was fixed on the chair 50 cm from the monkey's eyes. Small moving light spots were projected onto the screen by means of an optical system and two mirrors moved by servomotors.

Full-field horizontal optokinetic stimulation was achieved by a vertical-stripe cylinder 120 cm in diameter and 110 cm high surrounding the monkey. The vertical axis of the stripe cylinder was exactly aligned to the axis of the rotating chair (Fig. 1). The inside of the cylinder was covered by vertical black and white stripes of equal widths and 1·15 deg or 2·3 deg period. The stripe patterns were produced by means of a silk-screen printing technique. They were illuminated by 'white' steady light. The luminance was between 10 and 70 cd m^{-2} for the white stripes; the black–white contrast was about 0·7. The optokinetic cylinder was rotated by a servomotor located above the experimental room. Since the rotation axes of the cylinder and the chair were precisely aligned, cylinder rotation could also be achieved by a rigid coupling of the stripe cylinder to the rotating chair. Cylinder rotation and chair rotation could be controlled independently, e.g. by applying the same frequency but different phase angles and/or different amplitudes. In comparing responses to optokinetic and vestibular stimuli, we selected stimuli with identical amplitudes and frequencies (Table 1). For simple large-field optokinetic stimulation in non-horizontal directions, a round disc of 90 cm diameter covered with black and white stripes of 3·5 cm period was moved by hand 50–70 cm in front of the monkey.

Head and trunk rotation

Sinusoidal head rotation with the trunk stationary was made possible by connecting the head holder axis to the axis of the rotating (when necessary also removable) cylinder while the trunk was fixed to the stationary chair. Similarly, when the cylinder was stationary and the chair rotated sinusoidally, the trunk could be rotated with the head fixed in space. These two stimulus conditions were applied in darkness or while the room light was turned on.

Somatosensory stimulation

To explore the somatosensory input of the neurones recorded, we used simple hand-moved stimuli: tapping the skin of the animal, applying light touch or stronger pressure, small pinches with a pair of forceps or pressure to individual muscles through the skin. During this stimulation the arms of the animals could be moved freely or were loosely held by the experimenter's hand. By this method painful stimuli were avoided, as these would have been noticed immediately by an aversive reaction of the animal. Passive movements of single joints were made and active grasping movements were aroused by showing small tantalizing objects (peanuts, raisins) to the monkey. The somatosensory stimuli were applied in the light and also in the dark to exclude additional visual cues aroused by the movements of the experimenter's hand.

Data analysis

Data stored on tape were later processed off-line by a HP digital computer (HP 1000). Average peristimulus time histograms (PSTHs) were computed, as a rule, by averaging the neuronal responses to eight to ten identical stimulus periods (sinusoidal rotation, etc.). From the PSTHs the

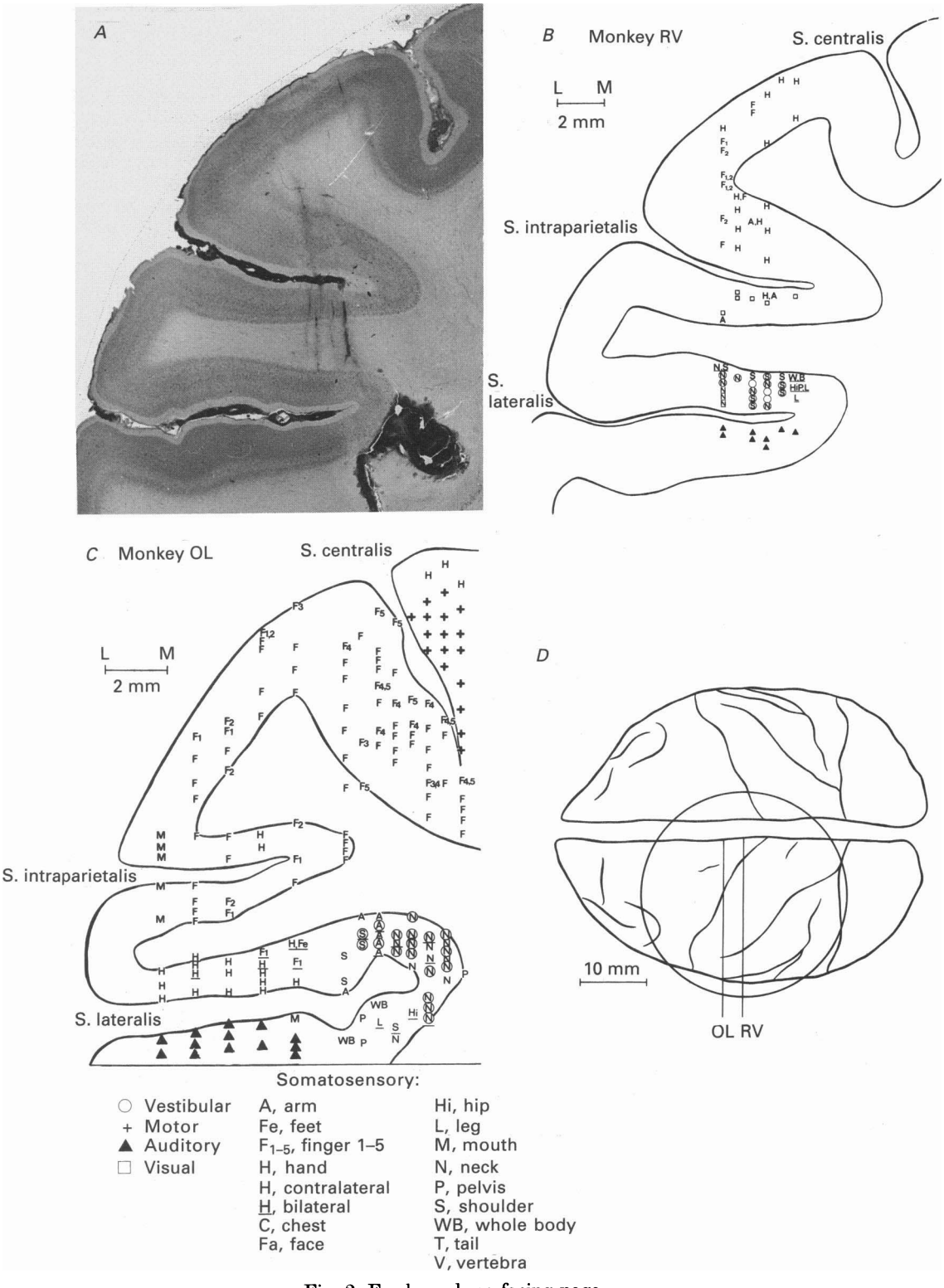

Fig. 2. For legend see facing page.

sinewave best fitting the experimental data was computed and its amplitude and phase used for further evaluations.

Reconstruction of electrode tracks and localization of recording sites

For all neurones including those recorded outside the vestibular cortex, the stereotaxic co-ordinates (anterior/posterior and depth related to the co-ordinates of the implanted cylinder) were recorded. At the end of each recording series with one monkey, a functional map could be reconstructed for the different coronal planes. During each final recording session, three to five thin needles (0·2 mm diameter) were inserted parallel to the most important microelectrode tracks. The position of these guide needles was used to find the different tracks on the histological slices and to achieve a congruent anatomical and functional reconstruction despite the tissue shrinkage due to histological fixation.

After the last experiment the monkey was anaesthetized with sodium pentobarbitone, given a large dose of heparin (1500 i.u.) through a femoral artery catheter and perfused with heparinized Ringer solution and 10% formaldehyde after a lethal dose of sodium pentobarbitone had been administered. Thereafter the top of the skull was removed and a photograph of the brain was taken with the dura mater still intact; a second photograph was taken following removal of the dura. These procedures facilitated the documentation of the sites where the microelectrode had penetrated the cortex and also allowed estimates of shrinkage due to the histological preparation. The brain was cut in serial microtome sections of 40 μm thickness and the individual electrode tracks were reconstructed from this series (frozen or paraffin-embedded material). For histological staining, neutral red Haematoxylin and Eosin were used. After the electrode tracks had been reconstructed, the provisional maps were replotted and correlated with the histological sections.

RESULTS

Localization of the parieto-insular vestibular cortex (PIVC)

In 529 electrode tracks more than 1000 neurones were identified, but many more encountered along the tracks; 152 neurones were found to be activated by vestibular stimulation. These 'vestibular' units were encountered at depths between 8 and 17 mm (related to the first cortical electrical activity) in the upper bank of the lateral sulcus around the posterior end of the insula, sometimes also within the upper posterior end of the insula. Typical electrode tracks leading to PIVC are depicted in Fig. 2. It shows reconstructions of tracks in coronal planes of two different monkeys, indicating the gross lateral extension of the circumscribed region where vestibular units were recorded. We have called this vestibular area parieto-insular vestibular cortex (PIVC) (Grüsser, Pause & Schreiter, 1982).

Careful mapping and exploration of receptive field properties of the neurones along the electrode track to the vestibular area was necessary for a functional reconstruction of the neighbourhood of our target area. This reconstruction facilitated the search for the vestibular area in later experiments since the stereotaxic co-ordinates of the target area varied in different monkeys.

For a better demonstration of the overall extension of the PIVC, reconstructions were drawn in the manner of Robinson & Burton (1980*a*, *b*, *c*, Fig. 3): for this figure

Fig. 2. Photomicrograph (*A*) of a coronal section showing the electrode tracks within the plane reconstructed in *B*. The two schematic coronal sections (*B* and *C*) were obtained from two different monkeys (OL and RV) in planes as indicated in *D*. Reconstruction of the electrode tracks and schematic characterization of the neuronal response types as indicated by the letters. In the histological slice of monkey RV the haematoma at the inner end of the lateral sulcus was caused by one of the 'landmark' needles inserted shortly before perfusion and was histologically without any sign of fibrinous organization.

the parietal and temporal opercula were unfolded. This procedure facilitated the representation of PIVC and its neighbouring areas. Each symbol in Fig. 3 represents the response properties of up to twenty neurones recorded in the grey matter, located below the respective symbols. The main clusters of vestibular neurones were found in the upper bank of the lateral sulcus at the transition of its opercular part into the retroinsular region. In every animal examined, vestibular neurones were also found within the most posterior and upper part of the insular cortex. Besides this region of dense vestibular representation some neurones responding to natural vestibular stimuli were found more posteriorly in the retroinsular region or more anteriorly in the parietal operculum. The reconstructions of Fig. 3 are restricted to the sites of vestibular neurones recorded in the region around the lateral sulcus. The overall stereotaxic co-ordinates of PIVC are anterior 4–12 mm, lateral 16–19 mm, vertical 3–6 mm corresponding to 12–17 mm depth from the cortical surface. Not shown in Fig. 2 are the coronal planes where non-vestibular, i.e. mainly somatosensory, neurones were found in the upper bank of the lateral sulcus. The most anterior tracks of Fig. 2 therefore delineate the anterior border of PIVC. As far as the posterior border is concerned, we cannot define the location limits of vestibular neurones scattered through the retroinsular part of the lateral sulcus, because only part of this brain region was explored systematically. Data obtained in two monkeys suggested the existence of a second separate visuo-vestibular field located more posteriorly to the main PIVC region. Before this question is settled, however, further experimental studies are necessary. Due to our limited knowledge of cytoarchitectonics we cannot judge whether our recordings of vestibular responses were entirely restricted to one distinct cytoarchitectonically homogeneous field, as described by Pandya & Sanides (1973) in Rhesus monkeys. Further studies on this matter are in preparation.

Cortical areas bordering on the PIVC

As displayed in Figs 2 and 3, only pure somatosensory neurones were recorded in the lateral and anterior surroundings of PIVC. They had relatively large receptive fields located predominantly in the skin of the contralateral body-half and they were activated either by light touch or pressure applied to the receptive field. A somatotopic map could be drawn only inconsistently because of individual differences between the animals. In general, arm, hand and face representations were found more anterior and lateral, the leg and feet (sometimes 'whole body' and 'visual approach') representation more posterior and medial. Posterior to PIVC, somatosensory units with a similar somatotopic arrangement were found intermingled with visual neurones. These visual units could be activated by sudden visual presentation of interesting objects, by certain movements of these objects and rarely by optokinetic stimulation. Caudal to the PIVC, i.e. within the insula, the temporal

Fig. 3. Reconstruction of the PIVC area and its surroundings in an 'unfolded' view of the insula, according to Robinson & Burton (1980*a*, *b*). The parietal operculum is folded upwards, the temporal operculum downwards. The diagrams summarize data obtained in three monkeys (RV, FP, OL). Every functional index (letters or symbols as in Fig. 2) represents a summary of the functional properties of cortical units recorded by the electrode in the underlying layers of the cortex. For clarity only three representative track rows outside the PIVC are shown in monkey OL. The small inset in *D* shows the part of the unfolded insular region represented in the other three graphs.

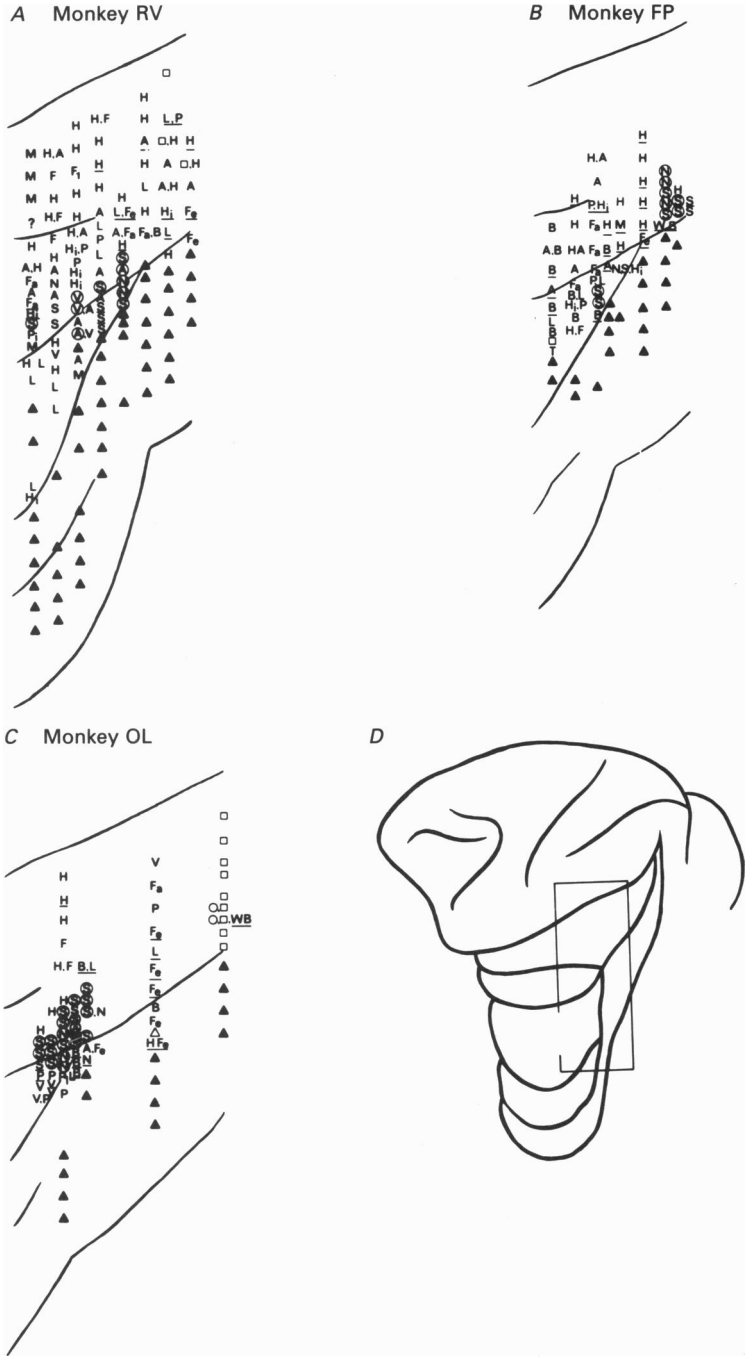

Fig. 3. For legend see facing page.

operculum and the lower bank of the lateral sulcus, auditory units were consistently found. They responded vigorously to noises like clapping, whistling or tone bursts, but rarely to stimulation of any other modality.

In summary, PIVC is located between a pure somatosensory and pure auditory region, immediately anterior to an area in which the neurones are also directionally selective to visual movement stimulation. Within PIVC some of the neurones are of the pure somatosensory response type, but the majority are multimodal vestibular units.

Despite an intensive search around the tip of the intraparietal sulcus (area 2v), we did not record a single vestibular neurone in this region, even in the additional four Java monkeys examined specifically for this purpose in an earlier study.

PIVC neurones are predominantly multimodal integration units

Of the 152 vestibular PIVC neurones, sixty-two were tested with horizontal optokinetic stimulation. All but four responded to this stimulus. Ninety-four units were examined with somatosensory stimulation. Most of them could be activated by mechanical stimulation of the neck and shoulder region, which will be described in a later report.

About 30% of all neurones recorded during one penetration of PIVC exhibited only somatosensory responses, very similar to those in PIVC neurones, but they had no direction-selective vestibular or optokinetic activation at all. This finding is important since one could argue that all vestibular responses are only somatosensory 'reflex' activations induced by muscle contraction (for example of the neck muscles) aroused by vestibular stimulation

Nearly all PIVC neurones were tested with simple auditory stimuli, but none responded. In a few neurones possible responses to a sound source rotating with the cylinder around the animal in the dark were explored. Again the result was negative.

Vestibular classification and spontaneous activity

PIVC neurones were classified as 'vestibular' when the investigator could clearly hear a neuronal impulse rate modulation synchronized with the sinusoidal rotation of the monkey chair in total darkness at 0·1–0·8 Hz and about 30 deg amplitude. In 145 of 152 neurones encountered in PIVC, averaged PSTHs were plotted. The remaining seven units were directly plotted with the ink-jet writer and had reproducible modulation amplitudes clearly above the criterion. A minimal sensitivity of 0·04 (impulses s^{-1}) (deg s^{-1})$^{-1}$ for horizontal sinusoidal rotation at 0·2 Hz, as calculated from the PSTH, was accepted to classify a unit as 'vestibular'. Most of the vestibular neurones, however, had a higher vestibular sensitivity. For those neurones activated only by pitch or roll stimulation, a minimal gain of 0·08 (impulses s^{-1}) (deg s^{-1})$^{-1}$ at 0·7 Hz was chosen for classification. As mainly horizontal stimulation was used in the search for vestibular neurones, units only activated by pitch or roll movements may have been missed.

The spontaneous impulse pattern of PIVC neurones was rather irregular. In addition, the spontaneous average impulse rate (averaging time 30 s) varied between different vestibular PIVC neurones from 1 to 15 impulses s^{-1}. As a rule, a general change in room illumination did not change spontaneous activity. When the animal became drowsy, however, the average spontaneous neuronal impulse rate decreased,

and concomitant with pendular or roving eye movements, clustered high-frequency discharges (doublets, triplets) appeared parallel to a decrease in vestibular responsiveness. When such conditions developed, the recordings were interrupted and the animal was wakened by some stimuli or by feeding. Thereafter eye

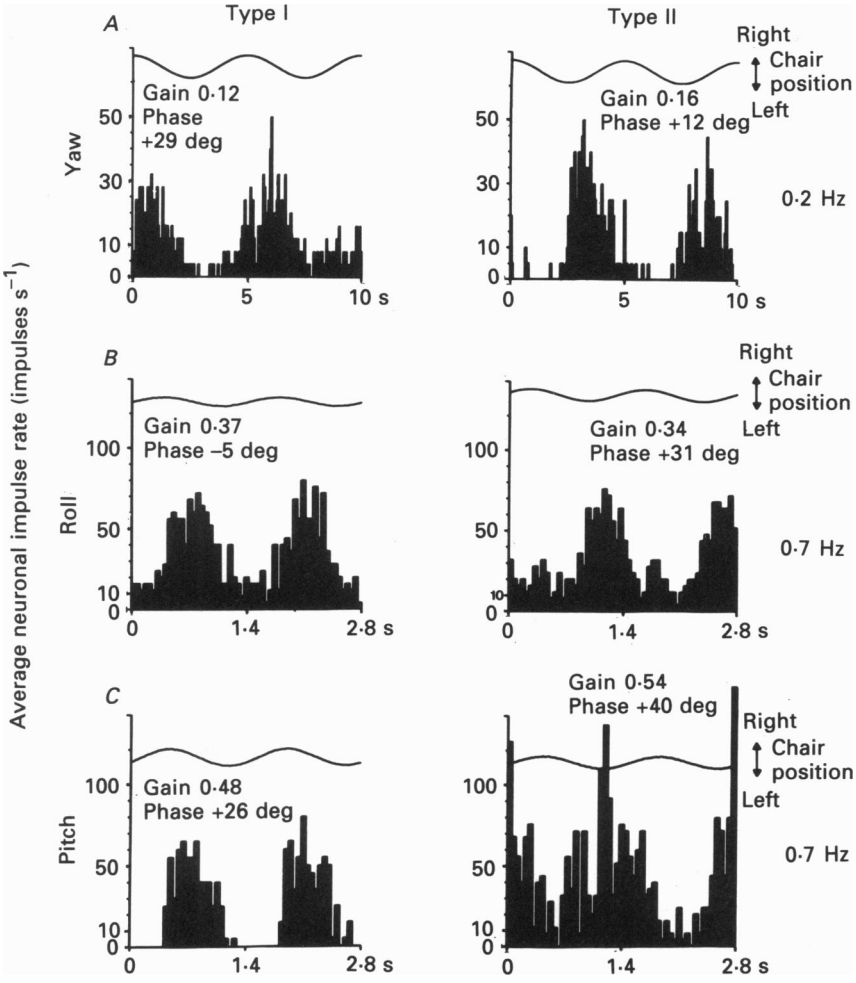

Fig. 4. PSTHs obtained in six different PIVC neurones of monkey OL exhibiting responses recorded during sinusoidal rotation in the three different experimental planes (yaw, roll and pitch). Neurones of opposing response types (type I on the left side, type II on the right side) are shown. Sinewave stimulus for horizontal rotation (yaw) was 0·2 Hz, 56 deg amplitude, for roll and pitch 0·7 Hz, 15 deg amplitude. Responses to ten stimulus cycles were averaged for the respective PSTHs.

movements and neuronal discharge rate usually returned to their previous level and recordings could be continued.

Responses to vestibular stimulation in darkness

In all vestibular PIVC neurones excitation or excitation and inhibition was observed during sinusoidal chair rotation or unidirectional angular acceleration and

deceleration in the dark. A pure inhibitory discharge (i.e. a reduction in spontaneous discharge only during a whole cycle of the vestibular stimulus) was never recorded. The possible association of the discharge modulation with the eye movements induced by the vestibular stimulation (VOR) is extensively discussed in the following article (Grüsser, Pause & Schreiter, 1990). In some neurones the modulation of the

TABLE 1. PIVC neurones: response type to sinewave rotation in different directions

	Yaw	Roll	Pitch
Neurones tested by stimulation in three orthogonal planes ($n = 18$)			
3 type	II	II	II
4 type	I	II	II
1 type	I	II	III
1 type	II	I	I
2 type	II	I	II
1 type	III	II	II
12 (67%) responded to stimulation in all three planes			
Neurones tested by stimulation in two orthogonal planes ($n = 46$)			
12 type	II	II	—
7 type	I	II	—
5 type	II	I	—
2 type	I	I	—
2 type	—	II	II
5 type	—	II	I
2 type	—	I	I
1 type	III	II	—
1 type	I	—	II
1 type	—	III	III
38 (83%) responded to stimulation in both planes tested			

impulse rate averaged with a bin width of 50–200 ms slowed down to 0 impulses s^{-1} during part of the stimulation cycle ('cut-off' responses). For classification of directional preponderance the scheme proposed by Duensing & Schäfer (1958) was applied: *type I* = activation during horizontal rotation (yaw, y) or roll (r) to the side *ipsilateral* to the recording site, *type II* = activation during rotation towards the *contralateral* side and *type III* = activation during rotation towards either side. For pitch-stimulation (p), type I neurones were those activated during 'nose-up' rotation, while type II neurones were activated during 'nose-down'. Of ninety-six units which modulated their discharge rate during horizontal sinewave rotations, thirty-six (38%) were type Iy, fifty-one (53%) were type IIy and nine (9%) were type IIIy. The directional preponderance of the eighty-eight units responding to vertical sinewave rotation ('roll') showed the following distribution: 35 (40%) type Ir, 50 (57%) type IIr and 3 (3%) type IIIr. The classification of those thirty-two units activated by the vertical 'pitch' stimulus resulted in nine (28%) type Ip, nineteen (59%) type IIp and four (13%) type IIIp. The most frequent responses in all rotational planes were type II, while type III responses were found very rarely. In Fig. 4 examples of PSTHs of type I and type II responses obtained in each of the three rotational planes are shown. The neurone in the left panel of Fig. 4*C*

demonstrates a typical 'cut-off' discharge pattern. It is evident from the description of the directional preponderance listed above that the majority of PIVC units were activated by rotation in more than one of the three experimental planes. Table 1 summarizes the combinations of directional preponderance in 'triaxial' and 'biaxial'

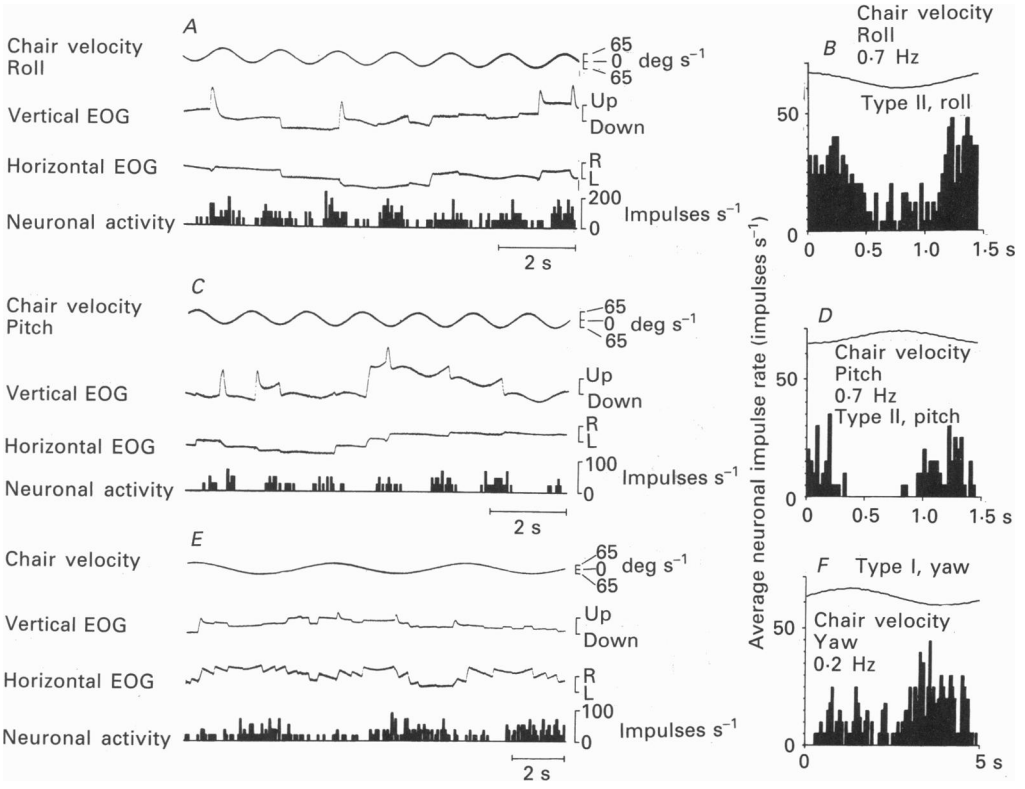

Fig. 5. Responses of PIVC neurone to sinewave rotation in roll (type II), pitch (type II) and yaw (type I) direction. Note the variability of the neuronal responses in the continuous recordings of neuronal activity (*A*, *C* and *E*). The average PSTHs (*B*, *D* and *F*) exhibit a much stronger activation during roll than during pitch rotation. Stimulation frequency 0·7 Hz, 15 deg amplitude for roll and pitch, 0·2 Hz, 15 deg amplitude for yaw.

neurones. From eighteen neurones tested with sinewave movement in all three stimulation planes, twelve exhibited a triaxial response, four a biaxial and two responded to rotation in only one plane. Forty-six neurones were tested in two stimulation planes only and thirty-eight of these neurones were activated by rotation in both stimulation planes. The remaining eighty-eight responding neurones were only tested by rotation in one plane, predominantly in the horizontal. Hence one can conclude that only a minority of PIVC neurones respond to vestibular stimulation in a single rotation plane only.

In the neurone shown in Fig. 5 the responses to vestibular stimulation with the same sinewave frequency and amplitude were investigated in all three experimental planes. Roll movement was clearly more effective than pitch rotation, which is visible in the different gains for roll stimulation (0·28 (impulses s^{-1}) (deg s^{-1})$^{-1}$) and for pitch stimulation (0·13 (impulses s^{-1}) (deg s^{-1})$^{-1}$) at 0·7 Hz. This neurone had a

type III response to horizontal rotation. It should therefore reach its maximum discharge rate during a roll rotation of the head to the right, with a slight bending forward. Because of the mechanical restriction of our stimulation equipment we could not test the responses to rotation in the expected optimum plane. Therefore these conclusions are only deductive ones and not based on direct observations.

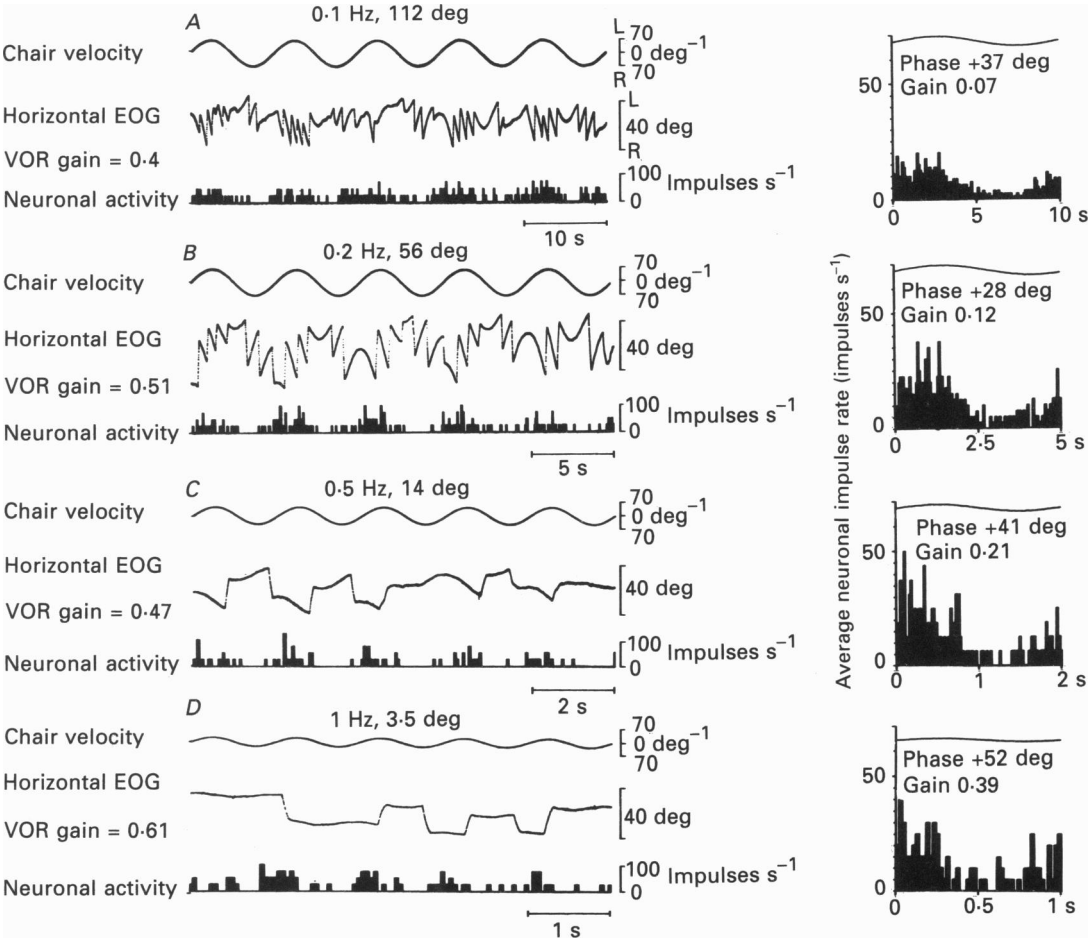

Fig. 6. Type I PIVC neurone responses to horizontal rotation (yaw) at different frequencies and amplitudes as indicated. The gain increased from 0·07 (impulses s^{-1}) $(deg\ s^{-1})^{-1}$ at 0·1 Hz to 0·3 (impulses s^{-1}) $(deg\ s^{-1})^{-1}$ at 1 Hz. This neurone was also activated by roll movement towards the left, horizontal optokinetic stimulation to the left, rotation of the trunk (head fixed) to the left and pressure exerted on the region around the sternocleidomastoideus muscle. Note the variability in neuronal responses in the continuous recordings, while the horizontal VOR visible in the EOG recording changed little. VOR gain was calculated by cutting off the saccades.

Gain and phase of neuronal responses to horizontal sinusoidal rotation in the dark

Figure 6 exhibits histograms of a type II PIVC neurone together with the vestibulo-ocular reflex (VOR) during horizontal rotation at different sinewave frequencies (0·1, 0·2, 0·5, 1·0 Hz, see Table 1). Several details from Fig. 6 should be

noted: (a) the relatively large fluctuation in the neuronal responses to identical stimuli as revealed by the continuously recorded impulse rate diagram (this behaviour was common to all PIVC neurones); (b) the increase in the average gain with increasing sinewave frequency within the range tested (0·07–0·39 (impulses s^{-1})

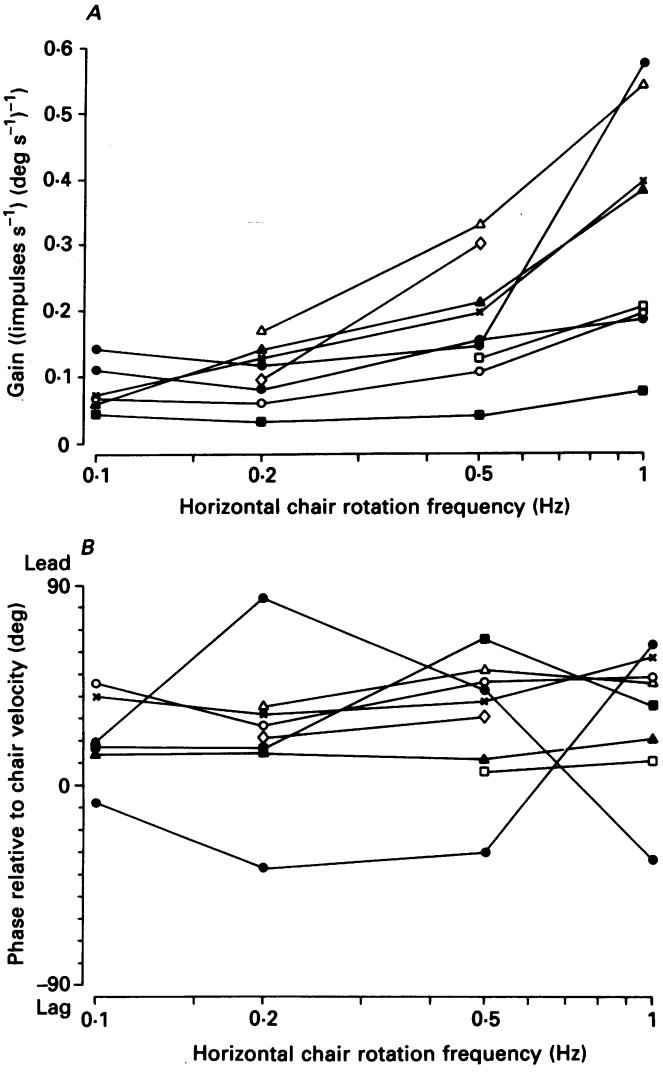

Fig. 7. Gain (*A*) and phase (*B*) response characteristics of nine PIVC neurones obtained with horizontal sinusoidal rotation (yaw) in darkness. Gain and phase values were obtained by fitting sinusoids to PSTHs. Gain increased with increasing stimulus frequency but phase did not change significantly between 0·1 and 1 Hz.

(deg s^{-1})$^{-1}$); (c) small changes in phase lead relative to maximal velocity of the responses with increasing stimulus frequency. The gain–frequency relationship is plotted for data obtained in nine neurones in Fig. 7; it indicates an overall increase in gain with increasing frequency, but the gain–frequency relationship exhibited a rather large variability between different neurones.

Most neurones did not exhibit any significant change in phase lead respective to velocity with an increase in stimulus frequency from 0·1 to 1·0 Hz (Fig. 7*B*). Figure 8 shows examples of the phase angle observed for the responses when sinewave stimuli were applied in the roll or pitch direction. With a 0·7 Hz stimulus frequency

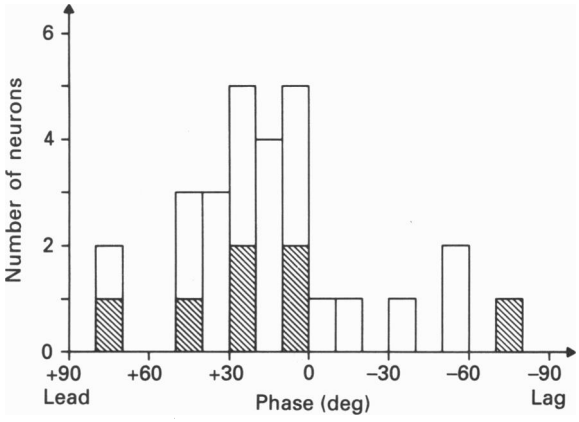

Fig. 8. Distribution of phase angle values obtained from PSTHs in twenty-eight different PIVC neurones for sinusoidal rotation in pitch (□) and roll (▨) direction (0·7 Hz, 15 deg amplitude in darkness).

of about 15 deg in amplitude, most of the PIVC neurones responded with a phase lead (relative to stimulus velocity) between 0 and +50 deg. With horizontal rotation (yaw stimulation) at 0·2 Hz the average ($n = 9$, of Fig. 7) phase lead of the neuronal response was 21·5 deg. We found no significant difference between type I and type II responses in the change in phase lag related to sinewave stimulus frequency.

DISCUSSION

Anatomical organization and connectivity of the parieto-insular cortex

The cytoarchitectonic parcelling of the parietal operculum, the retroinsular part of the lateral sulcus and the insula are not uniformly described. While Pandya & Sanides (1973) divide the upper bank of the Sylvian fissure into *proS* (posterior part of the parietal operculum) and the neighbouring *reipt* (retroinsular–parietal cortex), Jones & Burton (1976) discriminate between area SII (mainly congruent with *proS*) and *Ri* (only partially congruent with *reipt*). Both authors discussed the possibility of a 'vestibular' representation within the insula or the parietal operculum respectively. Jones & Burton (1976) proposed the insular dysgranular field (*Id*) as a candidate for vestibular representation because of its afferent connections from the ventro-posterior-inferior thalamic nucleus (VPI), which itself receives afferents from the vestibular nuclei (Lang, Büttner-Ennever & Büttner, 1979). Pandya & Sanides (1973), however, assumed the area *reipt* to be a possible vestibular projection area because it is considered to be cytoarchitectonically homologous to the area ASSS (anterior supra-Sylvian sulcus) of the cat cortex, where many investigators (e.g. Walzl & Mountcastle, 1949; Grüsser, Grüsser-Cornehls & Saur, 1959; Mergner, 1979) recorded vestibular responses. Some further evidence for the latter proposal was discussed by Mesulam & Pandya (1973), who found a small circumscribed 'patchy'

projection to *reipt* from the magnocellular division of the medial geniculate nucleus (MGmc) and projections from the ventro-posterio-inferior thalamic nucleus (VPI), both sites known to have a vestibular function. Pandya & Sanides (1973) also predicted that the presumed vestibular cortex in *reipt* is a polysensory area because it does not show the typical koniocortex of a primary sensory cortical area.

Comparing the location of PIVC neurones in our schematized reconstructions with the extension of *reipt* and *Ri* as shown in the drawings of Burton & Jones (1976), Robinson & Burton (1980*a*), Pandya & Sanides (1973) and Mesulam & Pandya (1973), obviously the majority of PIVC neurones was recorded within *reipt* (or *Ri*) and in the transition zones between SII, *Ri* and *Ig* (insular granular field). Therefore the recordings from PIVC apparently confirm the prediction of a vestibular projection by Pandya & Sanides (1973). In area *Id* (which was penetrated with many tracks) we could not find vestibular responses. This is congruent with the results of Sudakov, McLean, Reeves & Marino (1971), as they also failed to record vestibular activation in the insular cortex. Concerning possible efferent connections from PIVC, the work of Lobeck, Lynch & Hayes (1983) suggests a projection to the superior colliculi.

Is PIVC identical with the cervical representation of SII?

The secondary somatosensory area SII, first described by Woolsey (1943), was precisely delineated recently by Jones & Burton (1976), Friedman, Jones & Burton (1980) and Robinson & Burton (1980*a*, *b*) anatomically as well as electrophysiologically. In this area, which comprises the largest part of the parietal operculum, the receptive fields are arranged rather in patches to depict the body. The most caudal segment of SII represents in sequential order the neck region–feet–trunk–arm–feet. If a comparison with the somatotopy which emerged in our experiments is made, the similarity is evident. At least a part of PIVC is congruent with the neck and shoulder (cervical) representation of SII. This assumption, however, contradicts the opinion of Robinson & Burton (1980*c*) that 'no neurone in SII had even the hint of non-somatic sensitivity'. They, of course, could not find vestibular responses without application of vestibular stimuli, but using visual movement stimuli they should have discovered the visual responses which we found in almost all vestibular PIVC neurones.

As mentioned in Results, the posterior limit of PIVC cannot be clearly defined, but certainly there were vestibular units recorded too far posteriorly to be located within the cervical representation of SII, surrounded by visual units and 'complex' somatosensory units which have characteristics similar to those units found in *reipt* by Leinonen (1980). To summarize, we assume that PIVC partly overlaps the cervical representation of SII but extends posteriorly into *reipt* (*Ri* respectively). More recently extensive studies of the Squirrel monkey (*Saimiri sciureus*) in our laboratory indicated that the cytoarchitectonic region *Ri* in this species is a multisensory vestibular cortical area (Akbarian *et al.* 1988).

Directional vestibular sensitivity of PIVC neurones

A comparison of the distribution of the directional vestibular sensitivity of PIVC neurones (yaw only) with the distribution in the ascending vestibular relay nuclei showed no statistically significant difference (χ^2 test). We counted 38% type I and

53% type II (9% type III) PIVC units, whereas Fuchs & Kimm (1979) found 43% type I and 57% type II and Buettner, Büttner & Henn (1978) recorded 44% type I and 56% type II units in the brain stem vestibular nuclei. Type III units were not observed in the vestibular nuclei, presumably because of the small sample of neurones. In the vestibular thalamic nuclei Büttner, Henn & Oswald (1977) classified 67% type I and 33% type II units. In area 2v Buettner & Büttner (1978) registered 50% type I and 48% type II responses. We conclude that the distribution of directional sensitivity is not essentially modified during signal transmission from the vestibular nuclei to the 'vestibular cortex'.

Comparison of gain and phase properties of vestibular neurones

Using methods similar to those applied by other authors (Buettner *et al.* 1978) we calculated the neuronal response gain by dividing the amplitudes of the sinewaves fitting best to the PSTHs by the respective maximal stimulus velocities (dimension: impulse rate/angular velocity ((impulses s^{-1}) (deg s^{-1})$^{-1}$). The average gain measured at 0·2 Hz (horizontal sinewave stimulus) was 0·11 (impulses s^{-1}) (deg s^{-1})$^{-1}$. This was significantly lower than the average gain of vestibular nuclei neurones described by Buettner *et al.* (1978) (0·77 (impulses s^{-1}) (deg s^{-1})$^{-1}$ at 0·1 Hz).·Büttner *et al.* (1977) calculated an average gain of 0·56 (impulses s^{-1}) (deg s^{-1})$^{-1}$ in the thalamic vestibular neurones. Evidently PIVC units are less sensitive to vestibular stimulation than the thalamic neurones (which were also recorded in untrained animals given amphetamines during the experimental sessions). The gain increase with increasing stimulus frequency, however, is similar in both regions. It was about 2 dB decade^{-1} (from 0·1 to 1·0 Hz). When gain is estimated from the published data of area 2v units from Büttner & Buettner (1978) the respective frequency-dependent values lie in a similar range: 0·06–0·5 (impulses s^{-1}) (deg s^{-1})$^{-1}$ gain increase from 0·1 to 1·0 Hz. With 0·2 Hz horizontal rotation an average phase lead of 21·5 deg respective angular velocity was calculated in PIVC neurones. Phase angles of thalamic vestibular neurones, 2v neurones and brain stem vestibular nuclei units show similar values. The distribution of phase angles did not change essentially in the pitch or roll planes. In summary, the most obvious differences between PIVC and the other 'vestibular' areas is the low modulation rate (sensitivity), whereas the transfer characteristics concerning gain and phase are similar.

Convergence from receptors located in orthogonal semicircular canals

The convergence of different canal afferents has been investigated systematically only by Abend (1981) in the vestibular nuclei of the squirrel monkey, where about 10% of the units could be activated by separate stimulation of two orthogonal canals. In his experiments none of the ninety-nine units responded to rotation in all three main planes. A high percentage (about 1/3) of the vestibular nuclei neurones showed convergence from otolith receptors and semicircular canal receptors. A similar convergence was found in cat vestibular neurones by Schor, Miller & Tomko (1984).

The percentage of convergence is quite different in PIVC, as very few units responded to stimulation in only one plane. We assume that there is a high degree of convergence from two or three orthogonal semicircular canals. This is congruent with Mergner's (1979) recording in the cat ASSS field where hardly any units

responding only to rotation in one of the three main experimental planes were found. Obviously on the ascending vestibular pathway interactions between primarily divided directional signals take place, creating an increasing complexity. Furthermore, in the face of these data, it should be pointed out that within PIVC all possible rotation planes of the head have a localized neural representation resembling the (visual) orientation distribution in the visual cortex (Hubel & Wiesel, 1977). Mergner's (1979) statement that 'coding angular velocity of rotation *in the different planes of space* might be one of the functions of the cat vestibular cortex (ASSS) neurones' could also be confirmed for the monkey with the one restriction that in our opinion *the different planes of rotation relative to the head co-ordinates* are encoded. Further arguments for this restriction will be presented in the following paper (Grüsser, Pause & Schreiter, 1990).

Conclusions

Based on our data we believe that we recorded from an area most probably homologous with the cat ASSS field and with the temporo-parietal vestibular area described by Penfield (1957) and Friberg *et al.* (1985) in man. We are not convinced that area 2v exists as a separate vestibular cortical field. Possibly scattered vestibular responses in area 7, which Kawano, Sasaki & Yamashita (1980) and we too recorded, were (mis)interpreted as a circumscribed projection. Concerning the transfer characteristics, the differences (lower sensitivity, higher convergence, higher variability of discharge) between subcortical vestibular areas and the PIVC region point to a progression to a more complex field, the proof of whose functional significance is still a matter of future research.

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